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A Guide to Pollen- and Seed-Cone Morphology of Black Spruce, White Spruce, Jack Pine and Eastern White Pine for Controlled Pollination

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Cover photograph:
A receptive seed cone
of white spruce.

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A Guide to Pollen- and Seed-Cone Morphology of Black Spruce, White Spruce, Jack Pine and Eastern White Pine for Controlled Pollination

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ABSTRACT

The paper describes pollen- and seed-cone morphology and development, pollen-cone collection for pollen extraction, pollen forcing, seed-cone stages for isolation and receptivity for pollination, the pollination mechanism, and pollination techniques in black *(Picea mariana)* and white spruce *(P. glauca)* and jack *(Pinus banksiana)* and eastern white pine *(P. strobus)*.

INTRODUCTION

The main function of seed orchards is to produce genetically improved seed for raising planting stock for reforestation. To produce quality seed, orchards are rogued to remove undesirable trees identified in progeny testing. Before roguing, controlled pollination based on mating designs is carried out on flowering trees to procure seed for progeny testing. When a mating design is to be carried out, a reliable forecast of pollen-cone (male cone, microsporangiate strobilus, microstrobilus) and seed-cone (female cone, megasporangiate strobilus, megastrobilus) production will facilitate the pollination. Mature pollen cones are picked for extraction of viable pollen for controlled and supplemental pollination, and filled seed production is maximized in each pollinated cone. Thus, a minimal number of seed cones is used per cross, and a maximal number of crosses can be made for a reproducing clone to complete a mating design.

In recent years, potted grafts have been used to induce or enhance cone production for breeding in a breeding hall. Also, accelerated growth has been carried out on potted seedlings to hasten their maturity for cone production in a greenhouse. These techniques will facilitate breeding and procurement of seed for progeny testing. In turn, accelerated growth of seedlings for progeny testing will shorten the cycles of advanced generation breeding for improvement of long-term tree crops.

Supplemental mass-pollination to open-pollinated seed cones increases filled seed yield by 1) supplementing insufficient pollen production in the orchard; 2) pollinating ovules which are not pollinated because of asynchronous flowering, the positions of seed cones in the crown, and the effect of prevailing wind; and 3) decreasing the incidental self-pollination where there is close proximity of the pollen and seed cones. If supplemental mass-pollination is to be effective, the correct timing of pollination with live, mature pollen is critical for maximal seed production.

Information in this report is intended to provide foresters with a guide to pollen- and seed-cone development in our bread-and-butter species in Ontario, namely, black *(Picea mariana)* and white spruce *(P. glauca)*, and jack *(Pinus banksiana)* and eastern white pine *(P. strobus)*. The description includes pollen- and seed-cone morphology and development, pollen-cone collection for pollen extraction, pollen forcing, seed-cone stages for isolation and receptivity for pollination, the pollination mechanism, and pollination techniques.

BLACK SPRUCE

Pollen Cones

Pollen-cone buds are usually borne in the lower two-thirds of a tree crown and are either terminal or axillary on the shoot. Overwinter pollen-cone buds are ovate and lustrous. Terminal pollen-cone buds have a few awl-shaped, fringed bud scales reaching the tip of the bud (Fig. 1) while axillary buds lack the awl-shaped scales (Fig. 2). Vegetative buds are ovate but more slender and have a dull rusty color. Terminal vegetative buds have many awl-shaped, fringed bud scales extending to the tip of the bud (Fig. 2), while the axillary buds lack the long bud scales (Fig. 2).

Inside the bud scales of an overwintering pollen-cone bud, the cone consists of a single axis bearing a series of spirally arranged microsporophylls, the pollen-forming appendages. Each microsporophyll has two microsporangia on the abaxial (lower) surface, and each microsporangium contains many pollen mother cells (PMCs). Meiosis in the PMCs begins in mid-April in southern Ontario and results in the formation of microspores. This microsporogenesis is followed by four mitotic divisions in the spores to form five-celled mature pollen (two degenerated prothallial cells, a

stalk cell, a body cell, and a tube cell) in pollen formation. The period from meiosis to the formation of mature pollen takes about one month.

During microsporogenesis, the pollen cone begins to enlarge, and eventually the tip of the cone breaks through the bud scales (Fig. 3). The pollen cone gradually emerges from the bud scales (Fig. 4), and at least three-quarters of the cone are out of the bud scales before it stops enlarging (Fig. 5). Soon after the pollen is mature, the cone axis elongates, partially exposing the microsporangia and forming a stalk at the base to separate the cone from the bud scales (Fig. 6). Pollen sheds when the dehiscence layer on each microsporangium splits open on a dry, warm day (Fig. 7). The peak of pollen shedding in southern Ontario usually occurs about May 20th. The day varies from year to year depending upon the weather.

The time to pick pollen cones for pollen extraction is after the pollen is mature and before it begins to shed. The last cell division in the pollen occurs when the stalk is elongating. Therefore, stalk elongation can be used as an indicator for pollen-cone picking. A flexible pollen-cone axis can also be used as an indicator. Often a cluster of pollen cones does not mature at the same time, but if one is mature and begins shedding, the rest are not far behind and can be picked. On a tree which receives full sunlight, the difference in pollen maturation between the south and north sides of the crown is minimal, whereas if the tree is shaded, the difference could be as much as three days. The period of pollen shedding in a tree may last about one week.

In a forest, it could take about a month from the first to the last pollen shedding, depending on the topography, the weather and the size of the cone crop. In an orchard where trees are from different stands of a wide geological area, most will shed pollen about the same time, but some early- and late-flowering clones could be a week apart in pollen shedding. Therefore, phenology of the selected trees should be taken into consideration when carrying out controlled and supplemental pollination.

Pollen cones should not be collected before pollen maturation because pollen production and viability will be low, and storability poor. Pollen forced too early often has decreased viability after a year of storage. If early forcing of pollen shedding has to be carried out, a large branch bearing pollen cones may be placed with the cut end in a pail of water and maintained at room temperature until pollen maturation. Forcing may be carried out as early as the first cell division in the pollen, but should be carried out as close to natural shedding as possible. If forcing is carried out on potted plants, do not bring them into a heated greenhouse until meiosis in the PMCs is completed. Forcing can also be performed by bagging a branch bearing pollen cones with a pollination bag about two weeks before natural pollen shedding.

Seed Cones

Overwintering seed-cone buds are ovolanceolate and lustrous. They are borne in the top one-third of the crown and can be terminal or axillary. Terminal seed-cone buds have a few awl-shaped, fringed bud scales reaching halfway to the tip of the bud (Fig. 9) whereas the axillary seed-cone buds lack these (Fig. 8).

Enclosed within the bud scales is a seed cone which consists of an axis bearing spirally arranged bracts, and an ovuliferous scale in the axil of each bract. At the base of an ovuliferous scale, two ovules attach to the adaxial (upper) surface. Upon fertilization, the ovules develop into seed. Seed cones average 27 fertile scales or 54 potential seeds per cone located in the mid-section of a cone, 19 infertile scales in the proximal end, and 12 in the distal end. In an overwintering bud, the ovule contains a single large megaspore mother cell.

In the spring, seed cones begin to grow and develop, and the buds become elliptic with light brown bud scales (Figs. 9, 10). At this stage, the buds are large and can be readily distinguished from

pollen-cone and vegetative buds. As the seed cone continues to enlarge, the tip of the cone emerges from the bud scales (Figs. 11, 12). The ovuliferous scales are nearly appressed when the seed cone is partially (Fig. 13) or just fully emerged from the bud scales (Fig. 14). The margins of the scales then become reflexed and the seed cone is fully receptive (Fig. 15). Controlled pollination should be carried out at this stage. The seed cone will stay receptive for about 10 days. The peak of seed cone receptivity synchronizes very well with the peak of pollen shedding. When the receptivity of a seed cone is about over, the margins of the scales in the proximal (basal) end of the cone close first, and this process proceeds to the distal end (tip) (Fig. 16). In some cases, the process is simultaneous for all the ovuliferous scales. When the margins of all the ovuliferous scales are straight, the cone is closed and is no longer receptive (Fig. 17). The change in the margins of the ovuliferous scales is the result of scale growth and ovule enlargement.

At the time of full receptivity (Fig. 15), each ovuliferous scale has two well-developed ovules, and the integumentary tip of each ovule has two long micropylar arms extending beyond the margin of the scale (Fig. 18). The arms of each ovule bend away from the cone axis (Figs. 19, 21) and toward the opening formed between adjacent ovuliferous scales (Fig. 15). Adjacent scales with their reflexed margins funnel pollen to the micropylar arms. Pollen grains land on the micropylar arms and adhere to the surface of the arms (Figs. 18, 19). Occasionally, some grains are found in the micropyle or in the pollen chamber on the surface of the nucellus (Fig. 20). The nucellus secretes a watery pollination drop which exudes between the arms and picks up any attached pollen. As the pollination drop evaporates, it is withdrawn into the micropyle, carrying the pollen to the pollen chamber. Not all the ovules in a receptive seed cone exude a pollination drop at the same time. Exudation occurs in the morning before sunrise. Pollen landing on the pollination drop causes the drop to be withdrawn by the ovule; the drop will not reappear again on that ovule. If there is no pollen, the drop will slowly and incompletely be withdrawn by the ovule after sunrise and a small drop will remain on the surface of the nucellus (Owens *et al.* 1987). The process of exudation will be repeated in the unpollinated ovule until the ovule is pollinated or the receptivity of the seed cone is over.

In controlled pollination, seed cones should be enclosed with pollination bags before any of their tips have emerged from the bud scales (Fig. 11). Pollen grains from early flowering clones could lodge on the bud scales of a seed-cone bud and on adjacent leaves and twigs before bagging. However, the chance for those grains to pollinate the flowering seed cones is remote. If isolation is carried out after the emergence of the tips of seed cones, there will be a risk of contamination from pollen grains landing on the ovuliferous scales (Fig. 13), then sifting down between the scales. This may result in fertilization of eggs and production of seed from unwanted pollen. On the other hand, seed cones should not be isolated too early, because heat in the bags will hasten their development and pollen may not be available for controlled pollination.

The number of seed cones which should be isolated in a pollination bag depends on the species and cone size. The number of bags required per cross depends upon pollen viability, pollination efficiency, mating design, and design of progeny testing. The optimal number of seed cones per bag ranges from five to 10 for black spruce. However, with this number of seed cones per bag, they will not all be receptive at the same time. If only one pollination is to be carried out for each bag, it is best to pollinate the seed cones when they are all receptive, since late pollination is favorable in spruces (Ho 1984). If two pollinations are to be carried out, the first should be done when more than 50% of the seed cones in a bag are receptive, and the second when all of the seed cones in the bag are receptive (some pollinated seed cones may have passed receptivity).

There are two types of controlled pollination technique. Syringe (or a similar device) pollination is most often used in forest tree breeding because of the low risk of contamination and ease of operation. However, the technique requires a lot of pollen since a cloud of pollen is forced into the bag by puffs of air. The technique is also inefficient and results in poor pollination efficiency and seed

production. The second method, brush pollination, is used most frequently by plant breeders in crop and horticultural science. The technique is not popular in forestry because there is a risk of contamination, and the operation is time-consuming. However, this technique requires little pollen, and is effective due to the close contact between the brush carrying the pollen and the seed cones. The technique is most suited to a young orchard where little pollen is produced and to a breeding hall when the environment is controlled.

Pollination bags are replaced with mesh bags to protect cones from insects after pollinated seed cones become pendant. Cones can be harvested when seed is mature in the first half of September in the year of pollination, or when seed begins to be shed in the mesh bags.

WHITE SPRUCE

Pollen Cones

Pollen-cone buds are either terminal or axillary and are borne in the lower two-thirds of the crown. Overwintering pollen-cone buds are ovate and lustrous, and can be differentiated from vegetative buds by their dull rusty color (Fig. 22). Although the shape and color of white spruce buds are similar to those of black spruce, white spruce buds are generally larger, and terminal buds lack awl-shaped bud scales. The young pollen cone inside the bud scales is similar to that of black spruce.

Meiosis in the PMCs begins in early April, and pollen shedding occurs about the 10th of May in southern Ontario. In the last 10 years, the earliest pollen shedding recorded was on May 1st and the latest on May 18th.

As meiosis begins, pollen cones enlarge and emerge from the bud scales. The bud scales break at their base and the proximal end of the pollen cone is exposed first (Fig. 23). The bud scales form a cap rest on the end tip of the cone (Fig. 24) until they are blown away by the wind (Fig. 25).

Elongation of the cone axis and formation of the stalk indicate that pollen (five cells) is mature and about to shed (Fig. 26). Pollen cones should be collected at this stage for pollen extraction.

Seed Cones

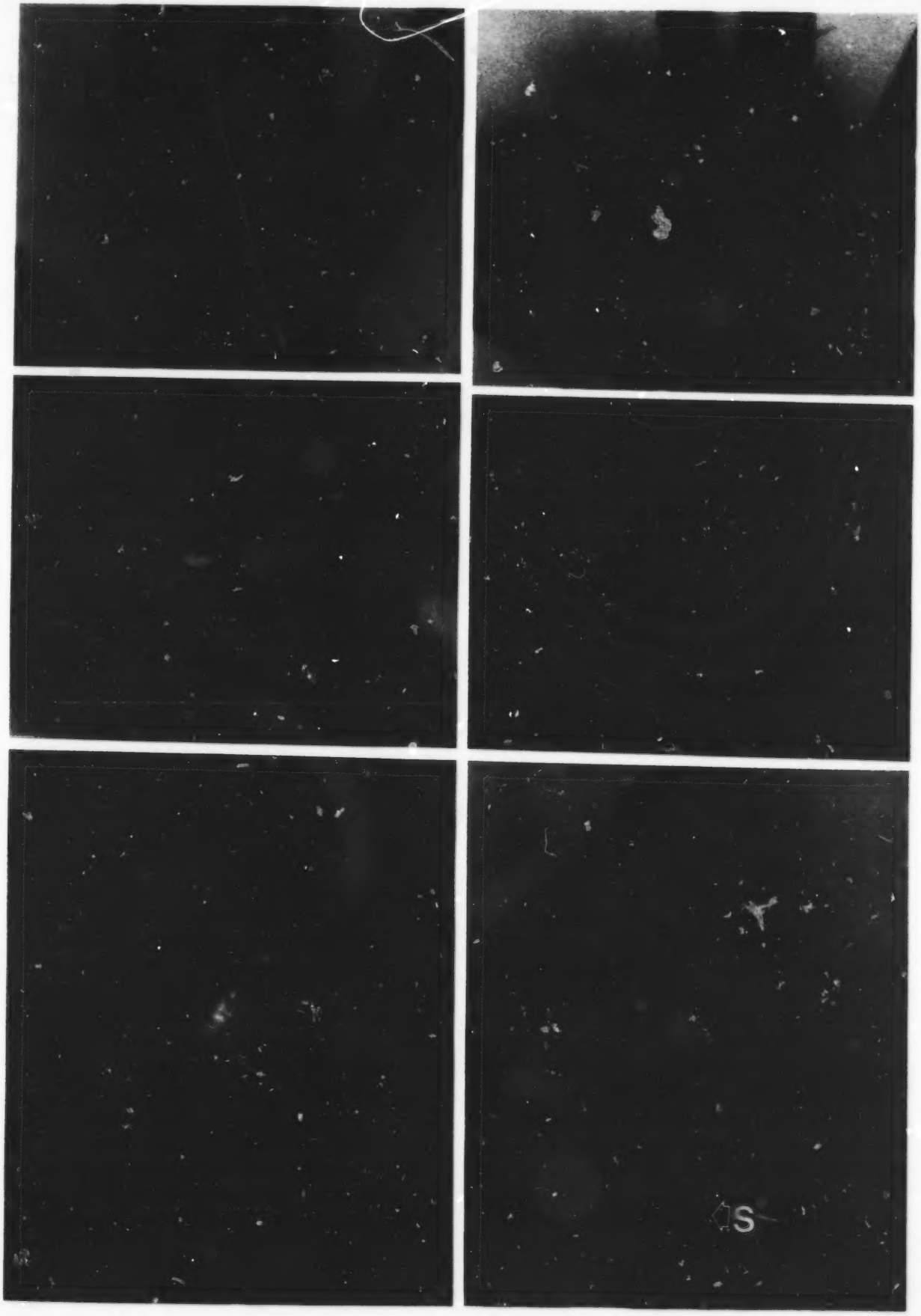
Overwintering seed-cone buds are ovolanceolate and lustrous (Fig. 27). They are generally borne in the upper one-third of the crown; however, in an open-grown tree in a good cone crop year, the crown may be covered with seed cones. The buds are either terminal or axillary and have no awl-shaped bud scales. Inside the bud scales, there are spirally arranged bracts and ovuliferous scales with two ovules, each ovule containing a megaspore mother cell, as described for black spruce.

Because of their size, shape and color, seed-cone buds can be easily differentiated from the pollen-cone and vegetative buds in the fall after all the buds have completed their development. In the spring, seed cones begin to enlarge and emerge from the bud scales in a manner similar to that described for the pollen-cone buds of white spruce. The ovuliferous scales on the lower half of a cone are exposed first (Fig. 28).

Seed cones emerge totally after discarding the cap of bud scales. At this stage seed cones are receptive (Fig. 29), but they do not reach the peak of receptivity until the margins of the ovuliferous scales are reflexed and the adjacent scales reflex to funnel pollen to the micropylar arms (Fig. 30). The pollination mechanism and seed-cone receptivity are similar to black spruce.

Occasionally seed cones at the peak of receptivity retain the cap of bud scales (Fig. 31). This could impede pollen entrance in the distal end. A few seed cones emerge first from the tip of a seed cone (Fig. 32) and others from both the tip and the proximal end of a seed cone (Fig. 33).

Figures 1-6. Black spruce pollen cones



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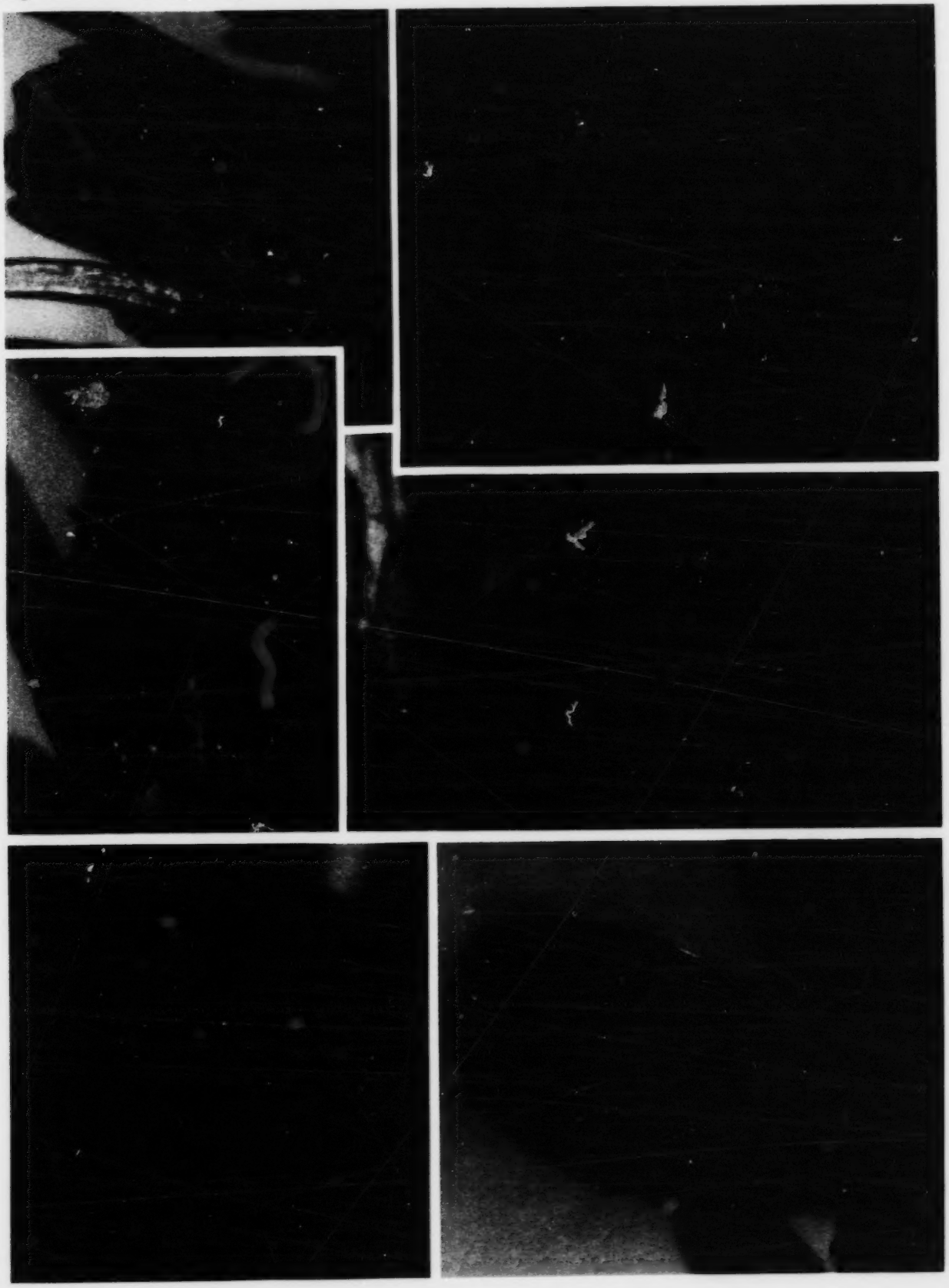

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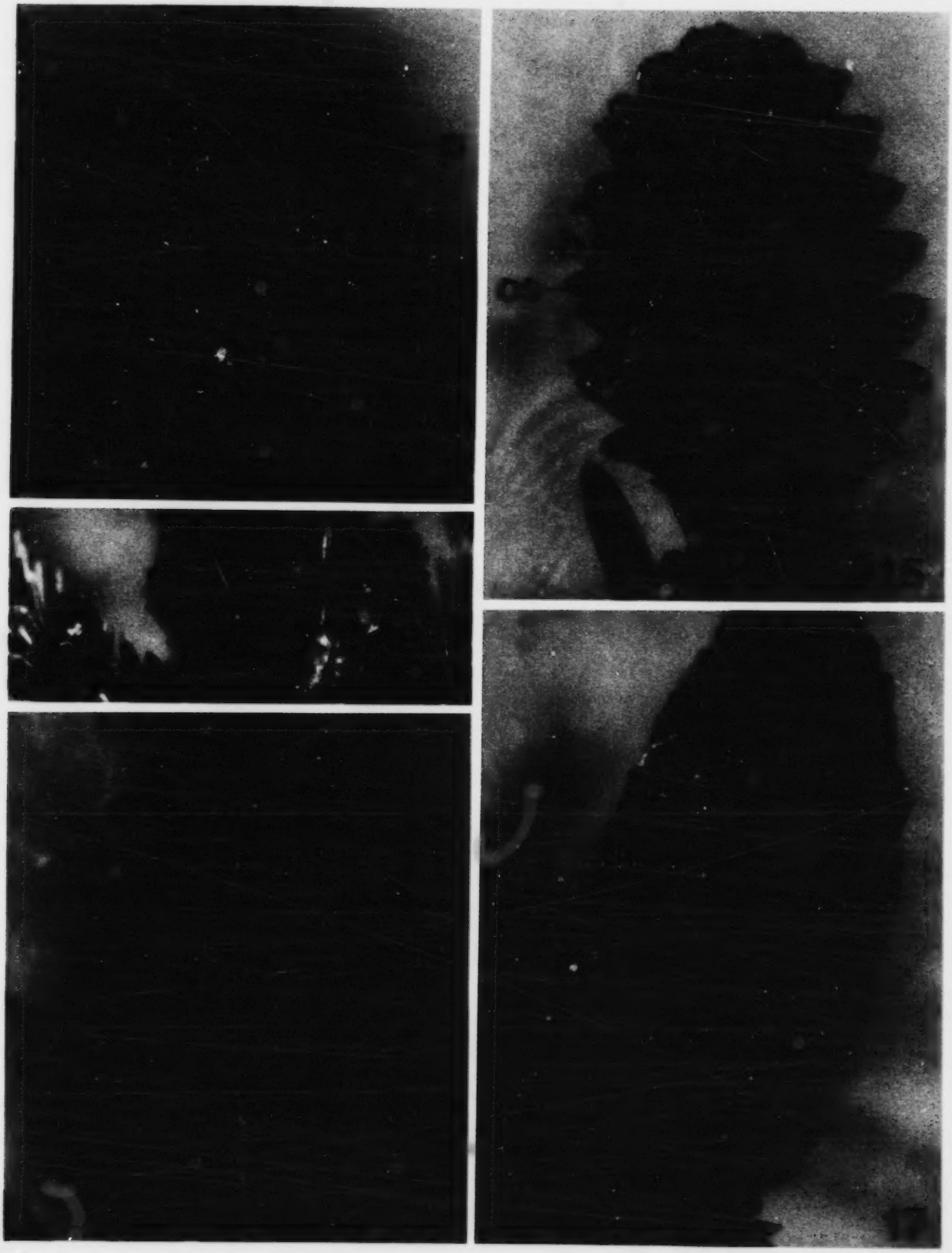

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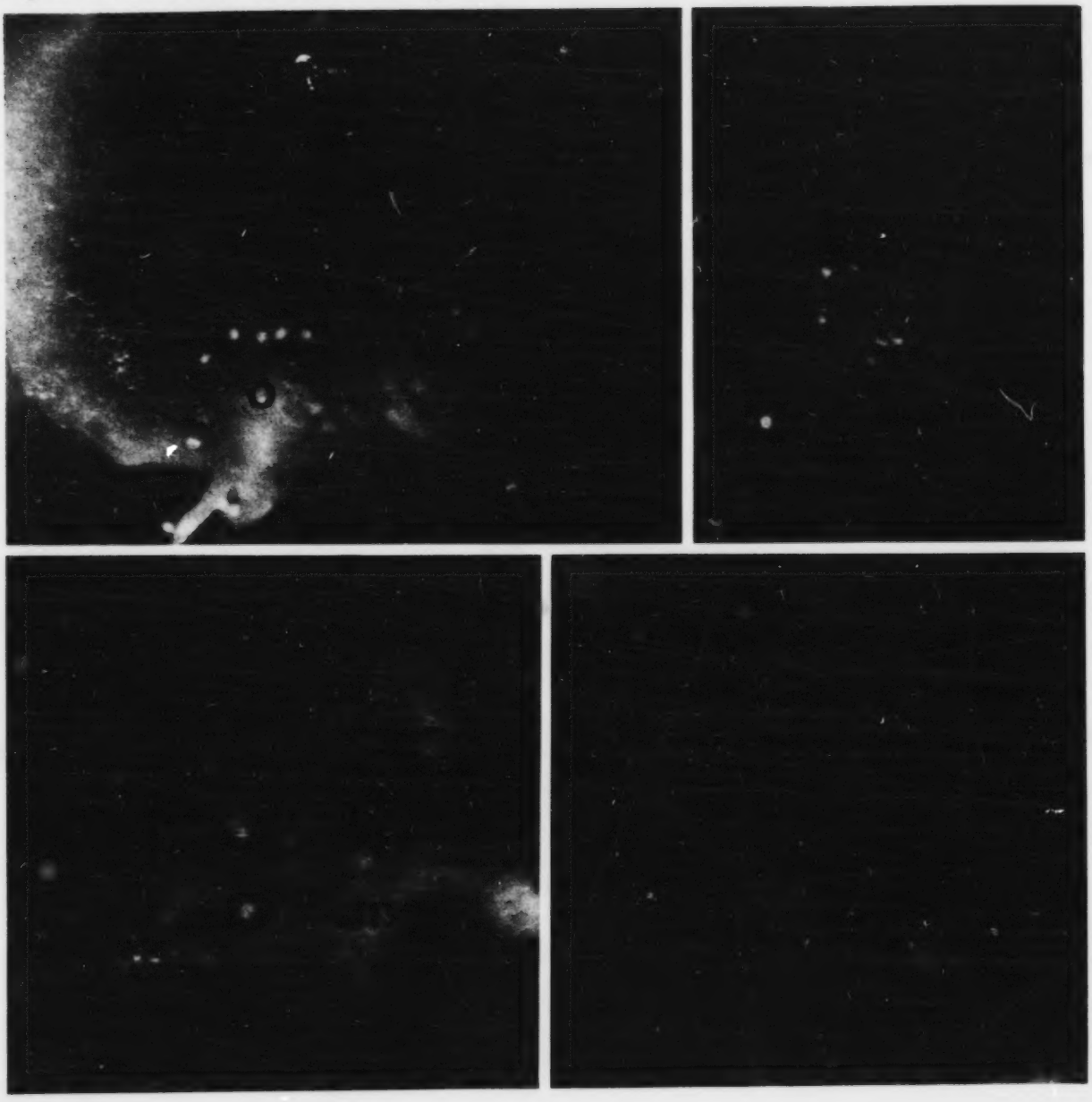

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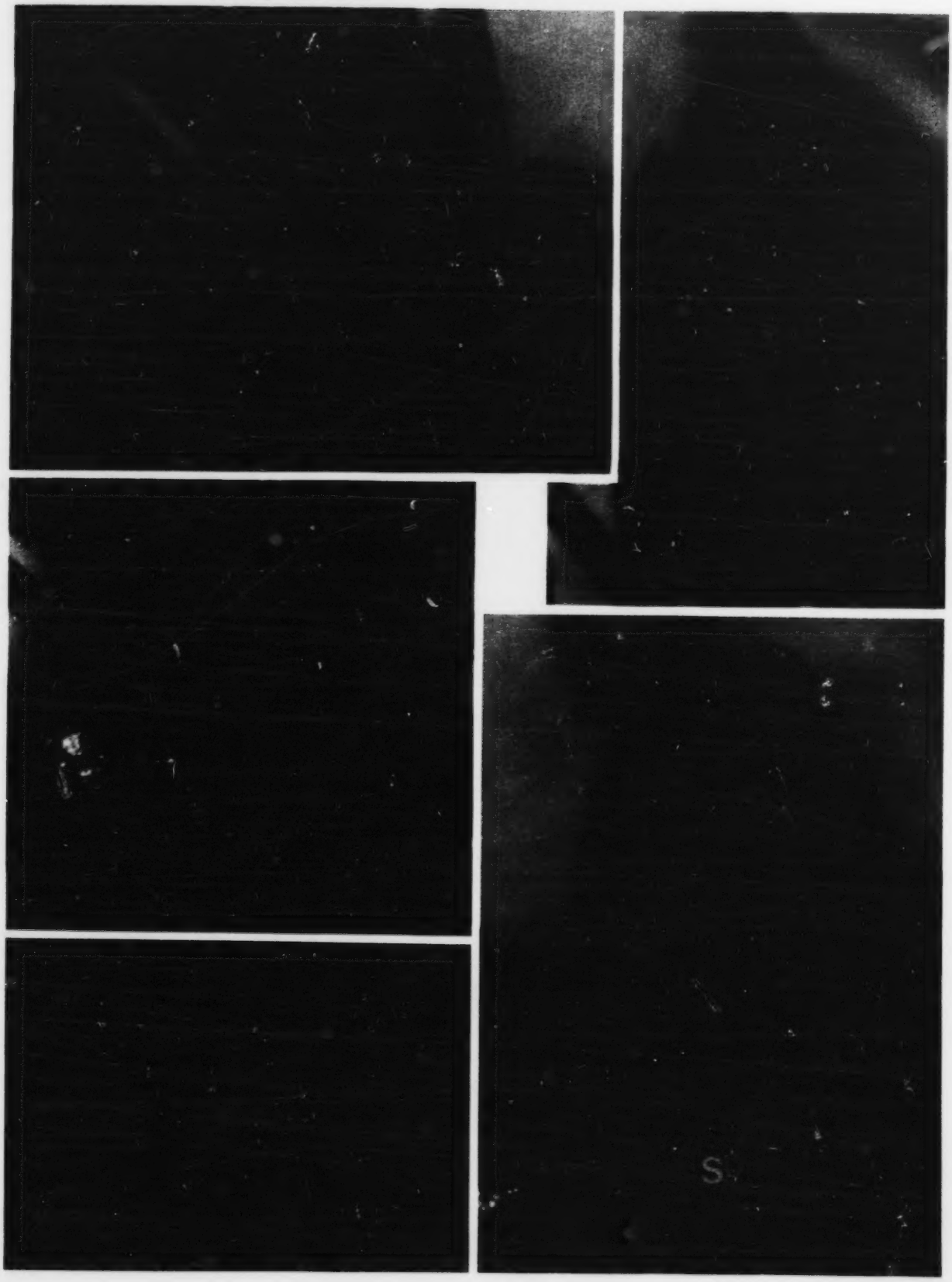

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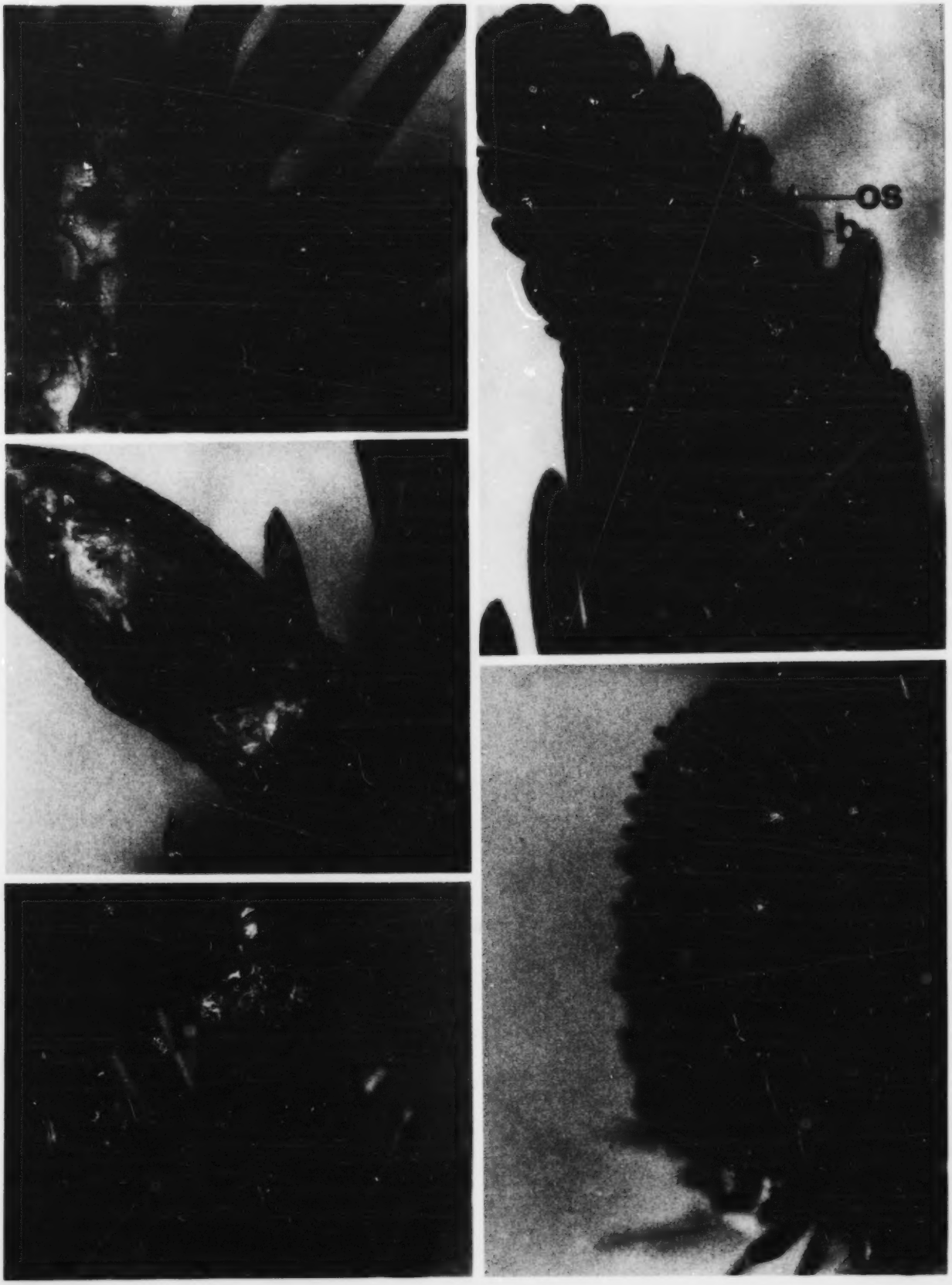

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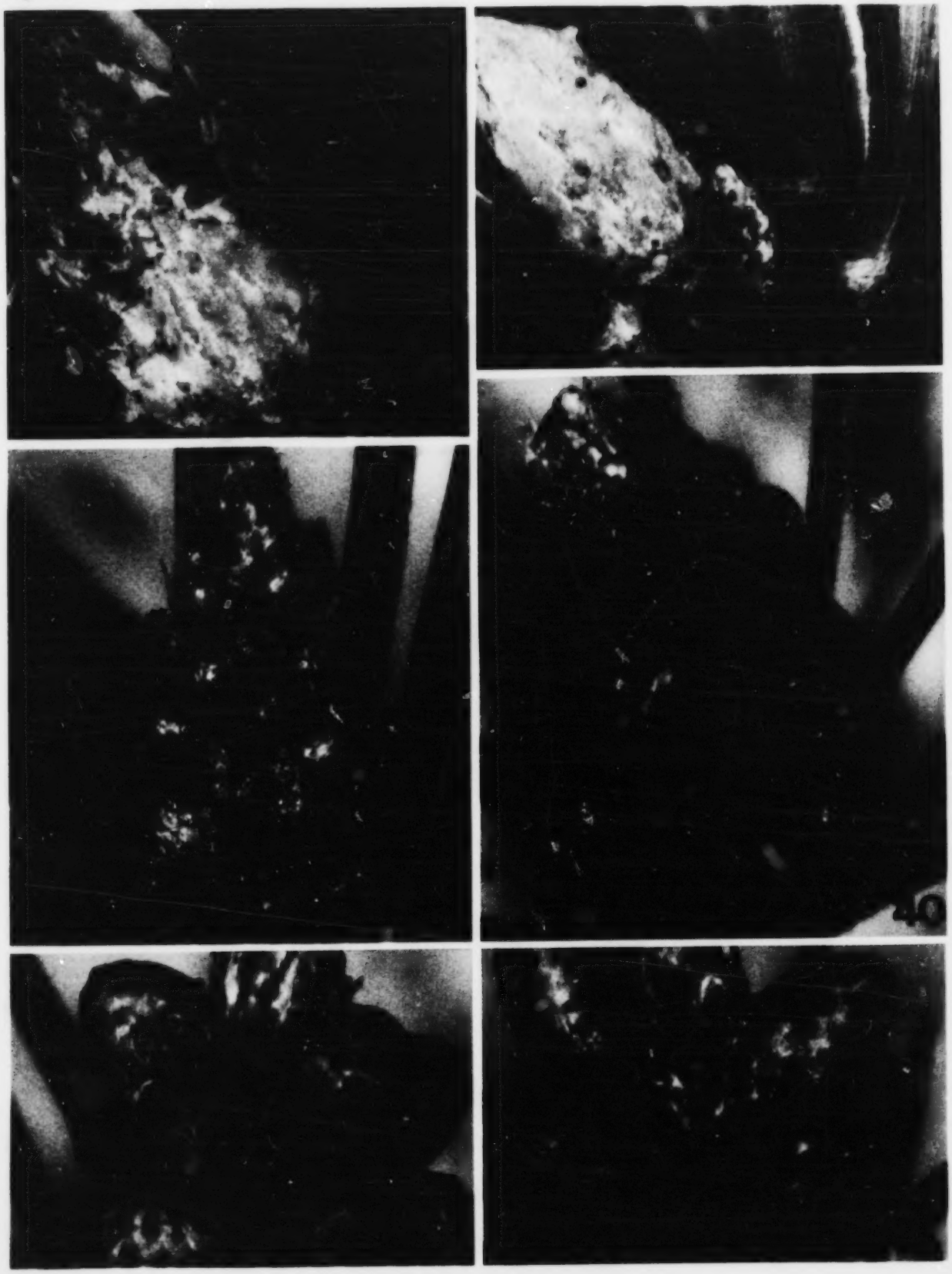

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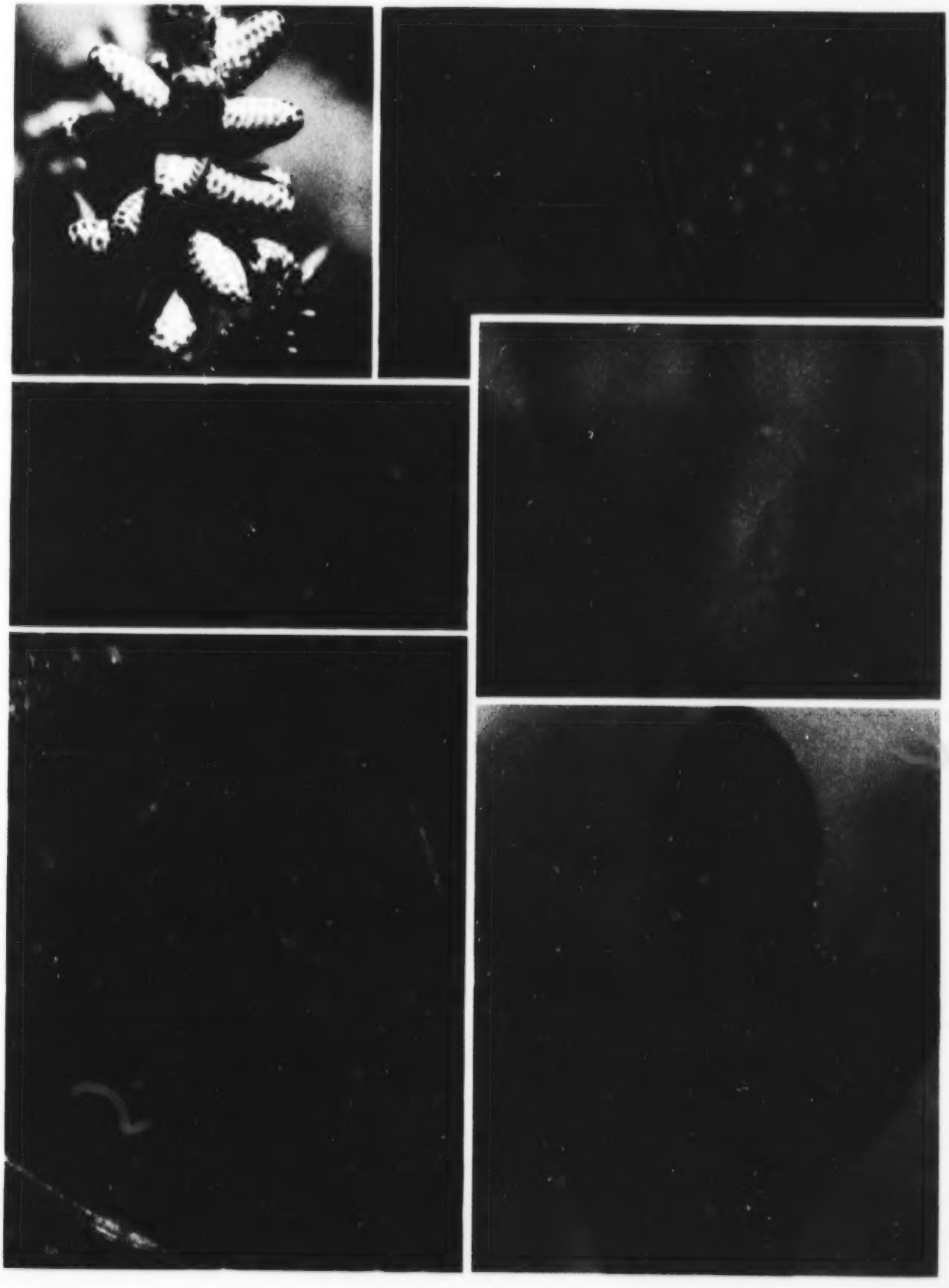

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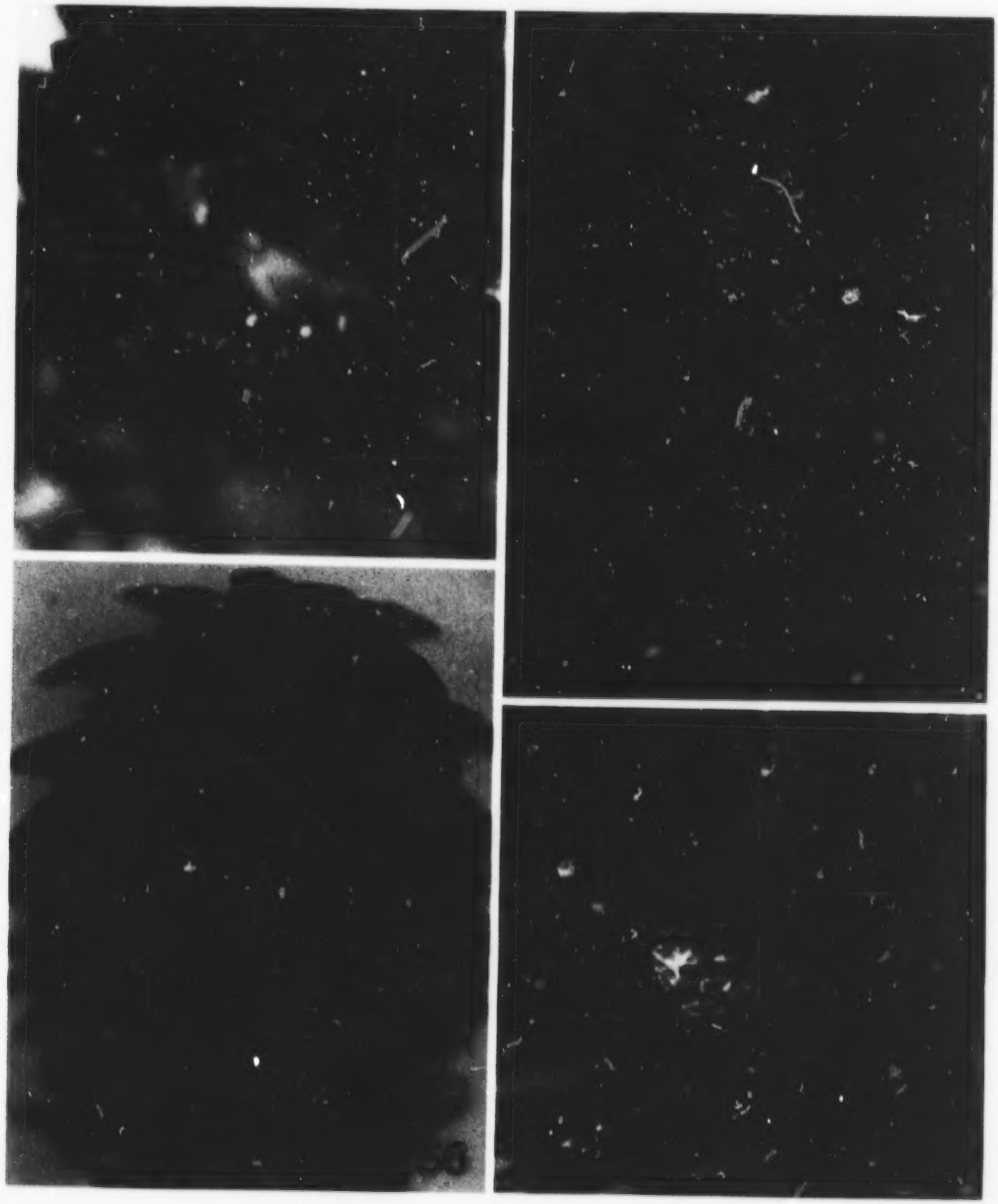

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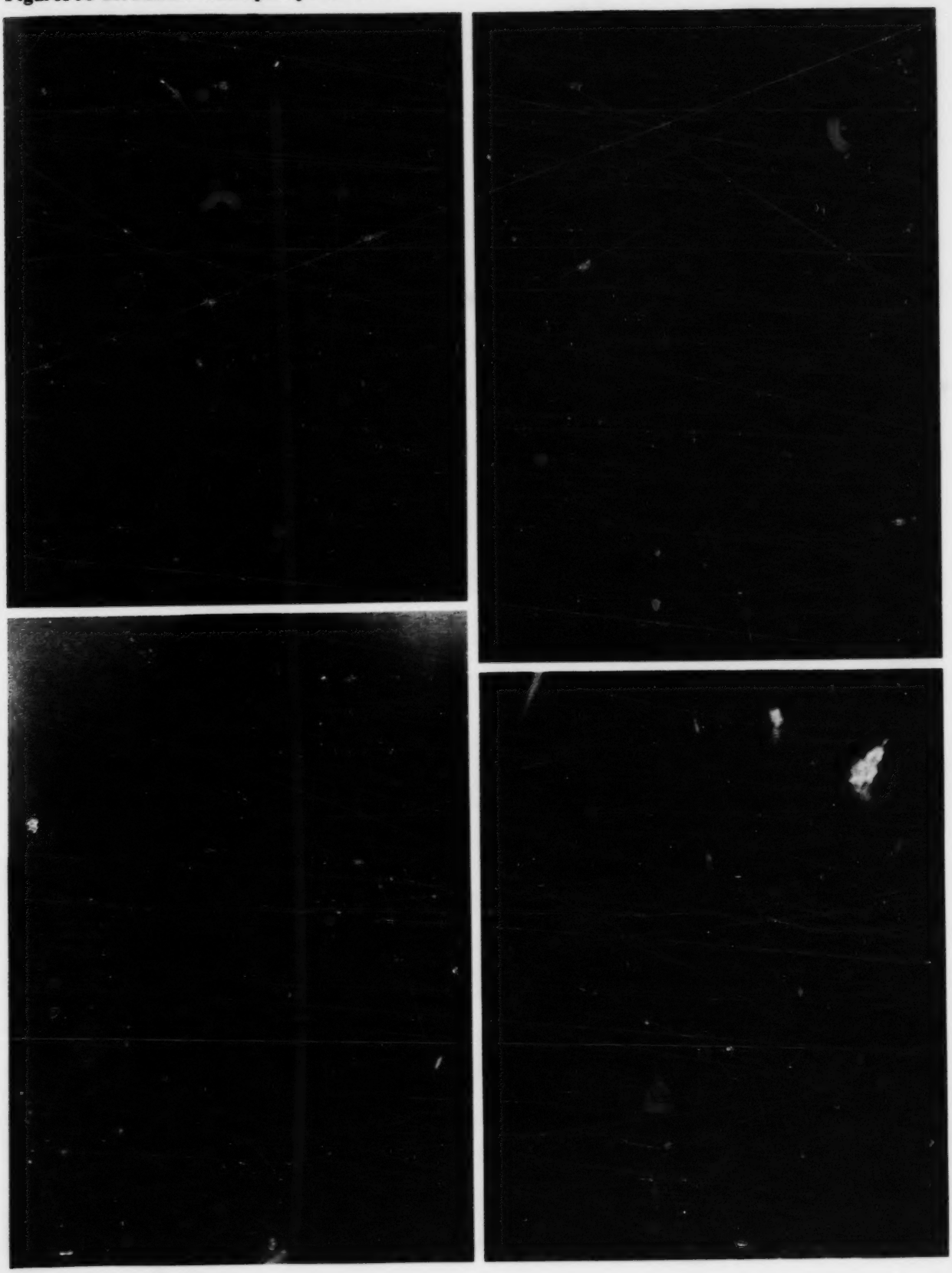

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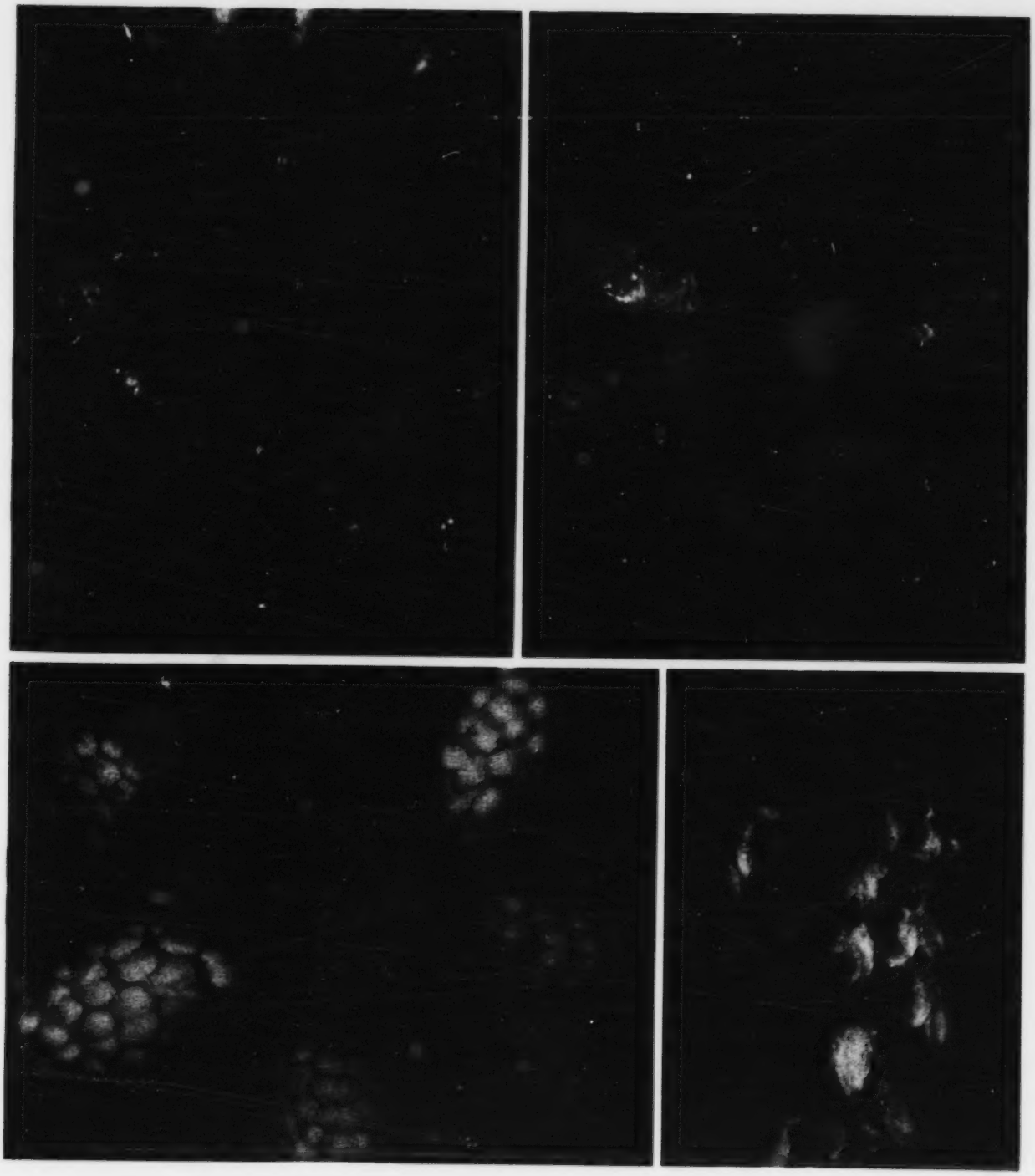

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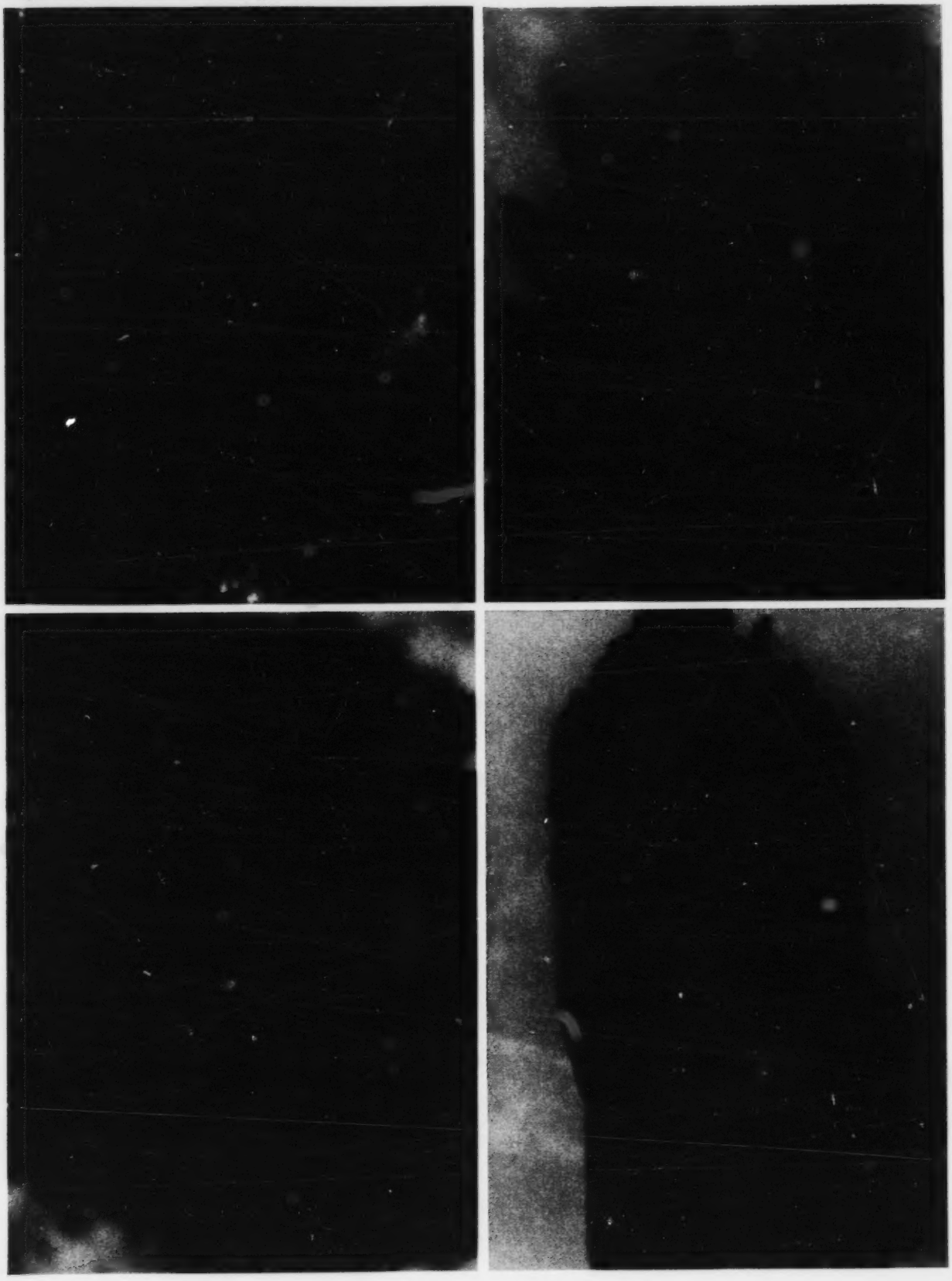

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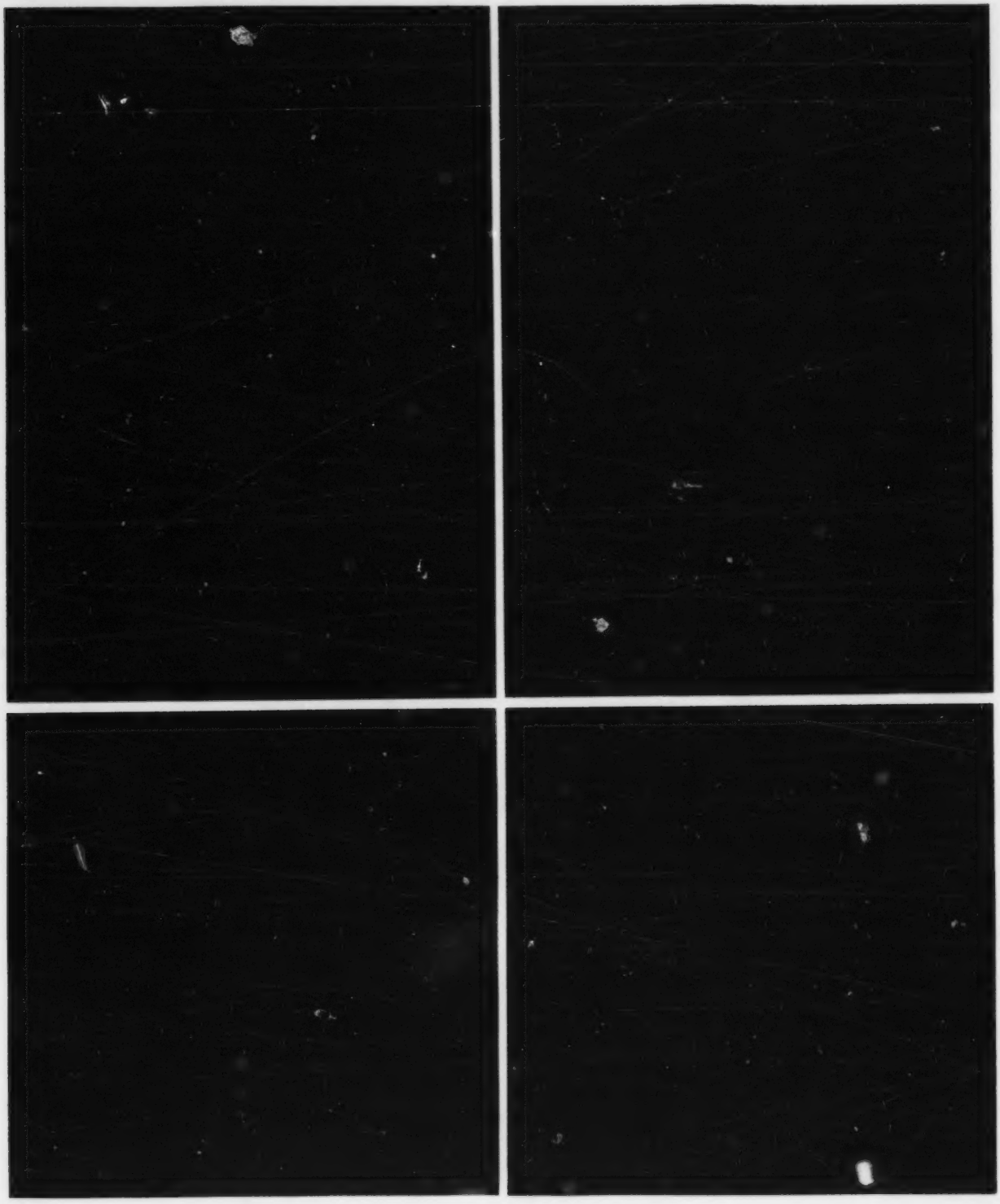
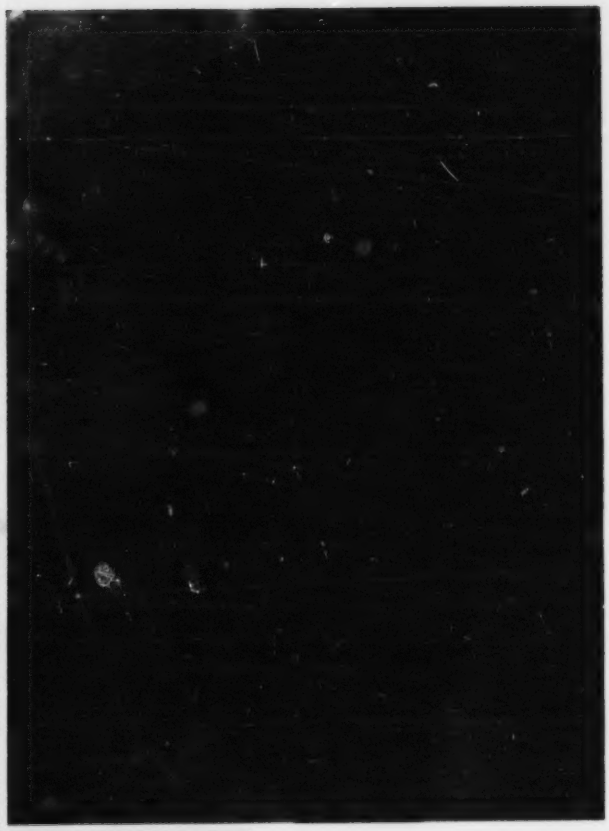


Figures 74-76. Eastern white pine seed cones



Timing of seed-cone isolation is more critical for white spruce than for black spruce because of the mode of cone emergence in white spruce. As in black spruce, isolation should be carried out before bud break. Five or fewer seed-cone buds should be isolated in a pollination bag for controlled pollination because the cones are large. Timing of pollination and the number of pollinations should follow the same guidelines as described for black spruce. When the receptivity of seed cones is over, the margins of the ovuliferous scales change from a reflex to a straight position (Fig. 34), followed by closing of the scales, which proceeds from the proximal to the distal end (Fig. 35). In some cases, the process is simultaneous for all the ovuliferous scales of a cone. As the ovuliferous scales close, the pathway for pollen to reach the ovules is blocked; this signals the end of receptivity (Fig. 36). About two weeks after the end of receptivity, cones become pendant, and three months later they are mature and can be harvested (second half of August).

Seed cones average 44 fertile scales or 88 potential seeds located in the mid-section of a cone, 11 infertile scales in the proximal end, and 13 infertile scales in the distal end.

JACK PINE

Pollen Cones

Pollen-cone buds are borne on the proximal (basal) region of a monocyclic long-shoot terminal bud (LSTB) of a less vigorous branch (Fig. 37). A monocyclic LSTB consists acropetally (from the base to the tip of a bud) of the bud scales of the current LSTB, a sterile region of cataphylls, a fertile region of pollen-cone buds or a region of dwarf shoots (needle bundles or needle fascicles), a second sterile region of cataphylls, a region of dwarf shoots, a third sterile region of cataphylls, a region with lateral vegetative buds or seed-cone buds, and a shoot apex covered by bud scales (Owens and Molder 1975). Because of the presence of pollen-cone buds, the reproductive LSTB has a much greater diameter than the vegetative LSTB (Fig. 38). A vegetative LSTB is often coated with resin (Fig. 38), while a reproductive LSTB with pollen-cone buds is often covered loosely with resin (Fig. 37).

Pollen-cone buds are axillary, one to a cataphyll. The number of pollen-cone buds per LSTB ranges from one to many. Based on a study in lodgepole pine *(P. contorta)*, the pollen-cone buds per LSTB averaged 20, ranging from one to 46 (Ho and Owens 1974). Each pollen-cone bud is covered by many bud scales. The cone consists of an axis bearing spirally arranged microsporophylls. Each microsporophyll has two microsporangia on the abaxial surface. In an overwintering bud, each microsporangium contains many sporogenous cells (Owens *et al.* 1981), in contrast to spruces which have many PMCs in each microsporangium.

Pollen-cone buds resume their development in the spring. The sporogenous cells divide to form PMCs followed by meiosis in the second half of April in southern Ontario. The buds enlarge and emerge from the cataphylls (Fig. 39). This is followed by the emergence of each pollen cone from the bud scales. The tip of a cone emerges first (Fig. 40). Enlargement continues until the cones are completely out of the bud scales (Figs. 41, 42). Prior to pollen shedding, the cone axis elongates to partially expose the microsporangia and the cone is greenish yellow (Figs. 43, 44). Pollen cones should be collected at this stage in order to obtain mature pollen for controlled pollination. Mature pollen has four cells - two prothallial cells, a generative cell and a tube cell. Pollen shedding occurs about May 23rd in southern Ontario and lasts for about one week (Figs. 45, 46).

Seed Cones

Seed-cone buds are usually borne on the distal end of a monocyclic LSTB of a vigorous branch. Seed-cone-bearing LSTBs are quite prominent with a distinctive swelling for each seed-cone bud (Fig.

47). Polycyclic LSTBs have more than one cycle of terminal bud growth. In polycyclic LSTB, seed-cone buds are not necessarily at the distal end and may occur in the mid-section of the LSTB (Figs. 48, 49).

Seed-cone buds are axillary to the cataphylls and inside the bud scales; each seed cone has an axis bearing spirally arranged bract primordia. No ovuliferous scales or ovules are formed in an overwinter bud (Owens *et al.* 1981).

Development resumes in the spring (Fig. 50) and bracts continue to be initiated in the distal one-third of a seed cone (Owens *et al.* 1981). Soon after the completion of bract initiation, ovuliferous scales are initiated in the axil of each bract. This is followed by the initiation of two ovules on the adaxial surface at the base of each ovuliferous scale. The tips appear first as the seed cones begin to emerge from the bud scales (Fig. 51). When a seed cone has half emerged from the bud scales, the bract-ovuliferous scale complexes are tightly packed, leaving little space between the complexes for pollen entrance (Fig. 52). When seed cones have fully emerged from the bud scales and some elongation of the cone axis has occurred (Fig. 53), the margins of the bracts are reflexed and seed cones are at their peak of receptivity. Controlled pollination should be carried out at this stage, which usually coincides with the peak of pollen shedding (about May 25).

In receptive seed cones, each ovuliferous scale has two well-developed ovules, and each ovule has an integumentary tip with two micropylar arms (Fig. 54). The arms are more slender than those in spruces. Large spaces occur between the bract-ovuliferous scale complexes to facilitate the entrance of pollen (Fig. 54). Jack pine does not have the funnelling mechanism described for spruces. However, jack pine is similar to spruces in the micropylar arm position, pollination drop exudation and withdrawal, and pollen pickup by the pollination drop.

The end of seed-cone receptivity is signalled by the thickening of ovuliferous scales causing closing (Fig. 55) and then sealing (Fig. 56) of the spaces between the bract-ovuliferous scale complexes. This ends receptivity since no more pollen can enter and land on the micropylar arms. Seed cone receptivity lasts about 10 days.

As in spruces, pollen grains landing on the micropylar arms are picked up by the pollination drop and transferred to the pollen chamber in the nucellus. Pollen germinates about two months after pollination (Owens *et al.* 1982). Each grain produces a pollen tube which grows about 300 microns into the nucellus before dormancy. In the following spring, the overwintering green cones (Fig. 57) begin to enlarge, and the pollen tubes resume elongation and reach and fertilize the egg in June. Cones are mature for harvesting in early September of the year following pollination. In jack pine, it takes about 13 months from pollination to fertilization, 27 months from pollination to cone harvest, and three years from seed-cone initiation to cone harvest.

Seed-cone buds should be isolated for controlled pollination before seed-cone emergence (Fig. 51). The number of seed-cone buds which should be isolated in a pollination bag for controlled pollination ranges from five to 10 because of small cone sizes. Brush pollination is advantageous because a single brushing can cover the entire cone.

Jack pine has a relatively short juvenile stage (in terms of reproduction) and begins to reproduce at about age five. When trees begin to reproduce, they are quite prolific. This is advantageous in shortening the breeding cycle.

EASTERN WHITE PINE

Pollen Cones

Long-shoot terminal buds (LSTBs) in eastern white pine are similar to those in jack pine except that there is only one sterile cataphyll region located at the proximal end of the LSTB (Owens and

Molder 1977). Cataphylls bearing pollen-cone buds are just above the sterile cataphyll region and each bud is axillary to a cataphyll (Figs. 58, 59). Pollen-cone buds are totally covered by the cataphylls; this fertile region can be differentiated from other regions by its swelling in the LSTB (Fig. 60). Pollen cones are produced on less vigorous branches and often in the lower two-thirds of the crown.

In an overwintering pollen-cone bud, all microsporophylls are initiated and arranged spirally on the cone axis before dormancy. No sporogenous cells are formed in the microsporangia of microsporophylls (Owens and Molder 1977). This is different from jack pine.

The LSTB begins to elongate and pollen-cone buds resume development in May (Fig. 61). Sporogenous cells are formed and meiosis occurs in mid-May as pollen cones begin to emerge from the bud scales (Fig. 62). Pollen cones have completely emerged from bud scales toward the end of May (Fig. 63). By June 10, the cone axis has elongated to form a space between microsporophylls and pollen begins shedding (Fig. 64). This is the stage at which to collect pollen cones for pollen extraction. Pollen shedding lasts for about a week, and when it is finished, microsporophylls shrivel (Fig. 65). The cones eventually fall to the forest floor. Mature pollen has four cells as described for jack pine.

Seed Cones

Seed-cone buds are not formed before dormancy (Owens and Molder 1977). Potential seed-cone buds are formed and present on the distal end of LSTBs. A potential seed-cone bud is axillary and has only a large apex covered by the bud scales. Therefore, they are not discernible at the distal end of the LSTB (Fig. 66) as they are in jack pine.

Seed-cone buds develop on vigorous branches in the upper crown and dominant branches in the lower crown. Resumption of development in the distal axillary apices on LSTBs occurs in April. The large apex of a potential seed-cone bud forms a large dome where no new bud scales are initiated, in contrast to a vegetative lateral bud where the small apex resumes bud-scale initiation (Owens and Molder 1977). Bracts begin to be initiated acropetally from the apex in early May, and by mid-May, ovuliferous scales begin to be initiated in the axils of the proximal bracts. At this stage, the seed-cone buds can be easily differentiated from the buds of dwarf shoots (Fig. 67). By early June, the distal end of the seed cone emerges from the bud scales (Fig. 68). If controlled pollination is to be carried out, seed-cone buds should be isolated prior to this stage so that there is no risk of contamination, although a few of the distal ovuliferous scales are infertile. The number of seed-cone buds which should be isolated in a pollination bag is five or fewer because of the larger cone sizes and seed production potential per cone.

When seed cones emerge from the bud scales, bracts and ovuliferous scales are straight (Fig. 69). Soon after total emergence of the seed cone, the margins of bracts become reflexed while the scales remain straight (Figs. 70, 71). Some elongation of the cone axis occurs to form a wide space between the bract-ovuliferous scale complexes, exposing the micropylar arms which have extended into the space. The scales, the reflexed bracts, and the ridge at the base of bracts conform to divert pollen towards the micropylar arms. This is the stage at which to carry out controlled pollination for maximal effect in procuring filled seed.

In a receptive seed cone, the two thin micropylar arms extend beyond the ovuliferous scales and bend away from the cone axis (Figs. 72, 73). The pollination mechanism is similar to that of spruces. The ovules exude pollination drops which pick up pollen grains that land on the micropylar arms. The drops are withdrawn by the ovules, carrying the grains to the pollen chamber in the nucellus. Pollen grains in the pollen chamber germinate about a month after pollination, and pollen tubes grow part way through the nucellus and become dormant in late summer (Owens and Molder 1977a).

A seed cone is receptive for about 10 days. During this period, the ovuliferous scales enlarge and eventually cover the micropylar arms and the space between the complexes, preventing pollen from reaching the arms (Fig. 74). This is the end of seed-cone receptivity. The ovuliferous scales thicken to seal the cone for the winter (Figs. 75, 76). Ovules and pollen tubes resume development in May after about eight months of dormancy. Fertilization occurs in early June, about 12 months after pollination (Owens and Molder 1977a). Cones are mature and can be harvested in early September of the year following pollination . Seed cones average 92 seeds per cone, or 46 fertile cone scales located in the mid-section of a cone, 22 infertile scales in the proximal end, and 7 infertile scales in the distal end.

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GLOSSARY

Abaxial: facing away from the axis.

Acropetal: from the base toward the apex; opposite of basipetal.

Adaxial: facing toward the axis.

Advanced generation breeding: progressive breeding of selected individuals from progenies of each generation.

Bract: leaf-like structure subtending a seed cone.

Bract-ovuliferous scale complex: structure which consists of an ovuliferous scale and the subtending bract which are often fused at the base.

Cataphyll: small scale-like leaf on the buds of pines often serving for protection.

Integument: outer cell layers of the ovule forming the seed coat.

Long-shoot terminal bud, (LSTB), monocyclic: a long-shoot bud consisting of one complete sequence of cataphylls and axillary structures terminated by seed cones or lateral branches.

Long-shoot terminal bud (LSTB), polycyclic: a long-shoot bud consisting of two or more sequences of cataphylls and axillary structures, each terminated by lateral branches or seed cones.

Mating design: mating scheme by crossing each tree with other trees in a group in order to obtain seed for progeny testing.

Megaspore mother cell: a cell that gives rise to female gametophytes (megagametophytes).

Micropyle: small opening in ovule formed by incomplete fusion of the integuments.

Micropylar arms: the slender extensions of the integument tip.

Microsporangium: the structure in which pollen grains are formed.

Microsporogenesis: the formation and maturation of microspores; the process proceeds from sporogenous cells to pollen mother cells, followed by meiotic division, tetrad formation, and finally spone maturation.

Microsporophyll: a foliar structure bearing two sporangia on the abaxial surface.

Nucellus: wall enclosing the female gametophyte in the ovule of seed plants. In the seed, the membrane beneath the seed coat is developed from the nucellus.

Ovuliferous scale: an ovule-bearing structure in the axil of a bract, forming the cone scale in a mature cone.

Pollen formation: the formation and maturation of pollen through three or four mitotic divisions within a microspore.

Pollen mother cell (PMC): a cell that is derived from the sporogenous cell and that gives rise by meiosis to four cells, each of which develops into a pollen grain.

Pollen viability: capability of growing and developing a pollen tube, often assessed by germination or vital staining.

Pollination efficiency: the number of ovules in a seed cone that are pollinated.

Progeny testing: a replicated experiment to compare the offspring of different parents, or to compare performance of offspring and parents.

Selfing: pollinating a seed cone with pollen from the same tree.

Sporogenous cell: a cell that is derived from the hypodermis of the microsporangium (pollen sac) and that gives rise to pollen mother cells.

Supplemental mass-pollination: supplementally pollinating unbagged seed cones with pollen, usually polymix, by a particle sprayer (pollinator or duster).